THE GENITALIA AND TERMINAL SEGMENTS OF THE MALE CARPENTER ANT, CAMPONOTUS PENNSYLVANICUS DEGEER (FORMICIDÆ, HYMENOPTERA)[1]

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This study describes and figures the external genitalic valves, the ninth and tenth abdominal terga, and the eighth and ninth sterna of the male Carpenter Ant, *C. pennsylvanicus* DeGeer.

Measurements have been taken for various parts of the structures described to compare *pennsylvanicus* with species of *Camponotus* described by Clausen (1938). The male genitalia as an aid in classifying ants is becoming more important now that more male ants are being associated with their corresponding workers and queens. Although the pattern of the genitalia is quite constant within the family and although the shapes of the individual parts of the genitalia are surprisingly similar within each genus, detailed studies are revealing important species differences (Clausen, 1938; Weber, 1947). Clausen found that subgenera of the genus *Formica* can be distinguished by genitalic differences and that genitalic differences are also found in species of the genera *Lasius* and *Camponotus*. Weber (1948) reports variations in one of the genitalic valves for some of the *Myrmica*.

In referring to the parts of the terminal segments, the terminology of Snodgrass (1941) has been used. Table I shows a comparison of the terminology of Snodgrass with that of Clausen.

The male ants for this study were collected from the same nests and at the same time as collections of ants were made for a previous anatomical and histological study of workers (Forbes, 1938). This investigation was begun shortly after the worker

[1] This name follows Creighton's "The Ants of North America." Formerly referred to as *Camponotus herculeanus pennsylvanicus* DeGeer.

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form was completed; the part concerned with measurements has been finished recently. The drawings for the paper have been made with the assistance of a Promar drawing apparatus (Siebert, Wetzlar).

TABLE I

COMPARISON OF THE TERMINOLOGY OF SNODGRASS (1941) AND CLAUSEN (1938)

Snodgrass	Clausen
Lamina annularis or Basal Ring	Cardo
Lamina parameralis or Basiparamere	Squamula
Paramere	Stipes
Cuspis volsellaris	Lacinia
Digitus volsellaris	Volsella
Lamina ædeagalis or Penis valve	Sagitta
——————[3]	Spatha

[3] Snodgrass has no term to indicate the spatha of Clausen, which is the lightly sclerotized, united, medial, dorsal margins of the laminæ ædeagales or the dorsal wall of the ædeagus.

OBSERVATIONS

The strongly sclerotized valves of the genitalia of *C. pennsylvanicus* project ventrally from the posterior end of the abdomen between the tenth tergum and the ninth sternum (fig. 7); the ninth and tenth terga are usually withdrawn beneath the eighth. The basal segment of the genitalia, the lamina annularis or basal ring, is roughly circular in shape. It is broad on its dorsal surface but is reduced to a narrow band on its ventral surface. The anterior margin of this basal ring is attached dorsally and dorsolaterally to the reflected ventral surfaces of the ninth and tenth terga, and it is attached ventrally and ventrolaterally to the posterior, intersegmental membrane of the ninth sternum. The posterior margin of the basal ring supports the three pairs of valves which constitute the genitalia (fig. 8).

Each of the outer pair of valves consists of a large, basal segment, the lamina parameralis, and a narrow, finger-like, distal extension, the paramere (fig. 12). The laminæ paramerales are laterally convex, they practically meet ventrally, and their dorsal proximal margins do touch (fig. 8). They partially ensheath

the middle and inner valves laterally and proximally. Sense pores and hairs are found chiefly on the ventral, median surfaces of the laminæ paramerales and around the distal ends of the parameres. Figure 11 indicates some of the variations of the dorsal margins of the outer valves. Measurements made on thirteen outer valves indicate variations as follows:

Portion of Valve	Minimum	Maximum	Average
total length (3)[4]	1036.8 μ	1188.0 μ	1109 μ
length of paramere (1)	496.8 μ	594.0 μ	536 μ
width of lamina parameralis (7)	594.0 μ	831.6 μ	694 μ

[4] The numeral or letter in parenthesis is the identifying symbol of the measurement as illustrated in text figure I. These symbols are used throughout the paper and have been chosen to agree with Clausen's designations except for those indicating measurements of the subgenital plate and the pygostyles.

Each of the middle pair of valves consists of a basal portion, the lamina volsellaris, from which a lateral and a median lobe extend distally (figs. 8 and 17). The lateral lobe is the cuspis volsellaris and the median lobe is the digitus volsellaris. The cuspis volsellaris is the shorter lobe, and its rounded, posterior end is directed dorsally. The large, blunt posterior end of the digitus volsellaris extends beyond the end of the cuspis lobe and is pointed ventrally and tilted slightly laterally. The middle pair of valves is assumed to be clasping segments because of the forceps-like arrangement of the cuspis and the digitus lobes (Wheeler, 1926, pp. 20–30) and because of the similar function of the middle pair of valves in other Hymenoptera (Snodgrass, pp. 22–24). The presence of small, sensory pegs, sensilla basiconica, on the opposing surfaces of the cuspis and the digitus further supports the idea of the clasping function of these lobes (fig. 8). Many sense pores are found at the distal end of the digitus, and sense hairs and sensory pores are found on the ventral surface of the lamina volsellaris and the cuspis lobe. Measurements made on eleven middle valves indicate that the length (VII) varies from 637.2 μ to 691.2 μ with an average of 663 μ. The distances between the caudal margins of the cuspis and the digitus volsellaris (V) is from 108.0 μ to 172.8 μ and

averages 147 μ. Variations in the distances between the dorsal margins of the cuspis and the digitus volsellaris (I) are from -16.2 μ to $+21.6$ μ with an average of $+1.5$ μ. A zero reading for this measurement would indicate that the dorsal margins of the two lobes are even or level; the minus reading indicates that the dorsal margin of the cuspis is situated ventral to the dorsal margin of the digitus, while a plus reading indicates that the dorsal margin of the cuspis is dorsal to the dorsal margin of the digitus. Clausen (p. 295) designates this measurement (I) as being taken between the "caudal" margins of these two lobes. The term "dorsal" is more appropriate. Clausen states in his description of the species of *Camponotus* (p. 332) that the dorsal margin of the cuspis does not reach the dorsal surface of the digitus volsellaris; he clearly shows this in his illustrations. Thus, according to the measurement scheme just explained, all Clausen's measurements for symbol (I) in Table II are negative in value. The observations on *pennsylvanicus* show that the dorsal margin of the cuspis, in practically all cases, is level with or slightly above the dorsal surface of the digitus volsellaris.

The inner pair of valves forms the ædeagus or intromittent organ and consists of two laterally compressed plates, the laminæ ædeagales. These plates are united dorsally by a lightly sclerotized membrane, the spatha of Clausen; the ventral and posterior margins are free (figs. 8 and 15). Each lamina ædeagalis has its greatest height proximally, and it tapers distally and ventrally to end in a slightly recurved hook (fig. 9). The ventral edge is serrate. A strongly sclerotized, prominent ædeagal apodeme supports the proximal, lateral wall of the lamina ædeagalis and projects anterolaterally. Many ædeagal muscles are attached to this apodeme. A number of sense pores are located on the posterior regions and the ventral margins of the laminæ ædeagales. These sensilla and some of the connecting nerve fibers which can be seen when examining these valves have been noted and figured by Adlerz (1886) for *C. ligniperda* and by Clausen for *Formica rufa*. The ejaculatory duct of the male reproductive system opens between the laminæ ædeagales at the dorsal, anterior region just beneath the membrane which unites the two valves dorsally. A fold of the upper,

median surface of each lamina ædeagalis forms a narrow furrow which extends the length of the valve and is roughly parallel with the dorsal edge. This fold, which I am naming the "sperm gutter," has not been described for any other ant, so far as I know (figs. 9, 15 and 16). These sperm gutters start on the inner surfaces of the laminæ ædeagales at the end of the ejaculatory duct. The median, proximal surfaces of the inner valves are joined vertically for just a very short distance below the ejaculatory duct. Measurements of ten inner valves shows variations as follows:

Portion of Valve	Minimum	Maximum	Average
total length (b)	561.6 μ	642.6 μ	603 μ
greatest width (c)	345.6 μ	453.6 μ	403 μ
length of serrate edge between first and last distinct tooth (e)	281.6 μ	372.6 μ	324 μ
number of distinct teeth (Z)	17	24	19.8

The ninth and tenth terga lie dorsal to the genitalia and are covered by the eighth tergum. The ninth tergum is separated medially and is arranged as lateral sclerites of the membranous tenth tergum (fig. 10). Snodgrass (p. 41) reports this formation for a *Formica* sp., and he describes similar arrangements of the ninth tergum for other ants. The anus opens on the posterior margin of the tenth segment, and the pygostyles arise from the posterolateral portions. The pygostyles are short, sclerotized, finger-like extensions of this segment which project beyond the caudal margin of the eighth tergum (fig. 7). The numerous sense hairs which cover the pygostyles are more abundant around the free ends. A large sense hair arises from the ventral, posterior region and curves slightly dorsally. Measurements of the lengths (M) of fourteen pygostyles show that they vary from 216.0 μ to 270.0 μ with an average length of 241 μ. Measurements of the widths (N) of eleven vary from 64.8 μ to 86.4 μ with an average width of 74 μ. Measurements of the thicknesses (T) of three taken across the dorsal surfaces show variations from 43.2 μ to 45.9 μ with an average thickness of 44 μ.

The eighth sternum is a large segment roughly rectangular in shape (figs. 7 and 18). The posterior, median margin curves slightly cranially. About eight prominent sense hairs are found in this posterior, median region. This segment is figured so that comparisons can be made with the figures of Clausen and Snodgrass for related ants.

TABLE II

SUMMARY OF MEASUREMENTS[5] OF THE GENITALIC VALVES AND THE TERMINAL SEGMENTS OF *Camponotus* SPECIES TO COMPARE MEASUREMENTS REPORTED BY CLAUSEN WITH MEASUREMENTS FOR *C. pennsylvanicus*

Segment	Symbol[6]	Measurements for *Camponotus* Species				
		Subgenus *Colobopsis: truncata*	Subgenus *Camponotus:*			
			vagus	*fallax*	*herculeanus*	*pennsylvanicus*
Half of Genitalia	A	21	13	27	53	142
	B	82	89	105	178	67
Inner Valve	a		115	123	267	279
	b	275	381	368	605	603
	c		246	275	427	403
	e		297	255	346	324
	Z[7]	14	18.5	16.6	19.88	19.8
Middle Valve	I	−16	−9	−16	−26	+1.5
	III	93	162	152	243	201
	V	27	65	87	128	147
	VII	239	342	346	516	663
Outer Valve	1	262	292	295	519	536
	3	485	644	637	997	1109
	4	64	134	127	135	178
	7	375	424	473	747	694
Subgenital Plate	W	514	510	805	900	957
	L	286	400	425	580	620

[5] All measurements expressed in micra except for symbol Z.
[6] The symbols are explained in the legend to PLATE XV.
[7] Number of distinct teeth on ventral margin of lamina ædeagalis.

The ninth sternum (figs. 7 and 14), which is also referred to as the subgenital plate, is shield-shaped with the median portion of its anterior margin extended cranially to form a marked projection. Figure 13 indicates variations of the cranial process of this segment. Usually six to eight prominent sense hairs are

found in the posterior, median region. Measurements of the widths (W) of twelve subgenital plates show variations from 864.0 μ to 1004.4 μ with an average width of 957 μ. Measurements of the lengths (L), excluding the cranial process, of a similar number vary from 572.4 μ to 691.2 μ with an average length of 620 μ.

DISCUSSION

The averages of measurements of the genitalia and the terminal segments described for *C. pennsylvanicus* are arranged in Table II together with similar measurements reported by Clausen for other species of the genus. A comparison of these averages indicates that *pennsylvanicus* is closer to *herculeanus* than to the other species listed; this is not surprising since these two forms are often grouped as subspecies of the same species. For these two species, the average measurements indicate that the genitalic valves of *pennsylvanicus* are longer and narrower than those of *herculeanus* and that the length of the lamina ædeagalis is practically the same for both.

Consideration was given to the size of the genitalia in relation to the overall body length. The genitalic measurements, as summarized from Table II, show *truncata* to be the smallest; *vagus* and *fallax* are approximately the same in size and are larger than *truncata; herculeanus* and *pennsylvanicus,* again approximately the same in size, are the largest. The papers of Wheeler (1910), Emery (1916), and Bondroit (1918) give the following body lengths for the males of these species: *truncata* 4–5 mm., *vagus* 9–11 mm., *fallax* 7–8 mm., *herculeanus* 8.5–11 mm., and *pennsylvanicus* 9–10 mm. Body lengths of *pennsylvanicus* males in the collection of the American Museum of Natural History and in my own collection fall within the limits reported. One male in my own collection, however, measures about 8.5 mm. These figures for body length shown *truncata* to be the shortest, *fallax* next, with *vagus, herculeanus* and *pennsylvanicus* all approximately the same and the longest. No definite conclusions are indicated by these comparisons. Whether a correlation exists can be determined only on the basis of a study of more species.

The arrangement of the cuspis and the digitus lobe of the

middle valve of *pennsylvanicus* together with the sensory pegs on the opposing surfaces of these lobes strongly suggests a clasping function. No published account could be found which gives the positions of the genital valves in *Camponotus* or other related forms in copula, nor are there immediately available copulating pairs from which to make observations. Clausen reports, after examining pairs of *M. scabrinodis* Nyl. and *M. rubra ruginodis* Nyl. which were captured and preserved in copula, that only the inner pair of valves is inserted into the vagina. The middle pair of valves and the parameres of the outer pair clasp the point of the female abdomen on either side of the female genital opening. The middle valve of *ruginodis* has a well developed cuspis lobe; this is not the case in all *Myrmica* species so far studied (Weber, 1948). Further observations by Clausen show the occurrence of sensory pegs or "warts" on the middle valves of various genera including *Camponotus*. These sensory pegs are absent on the middle valves of *Myrmica rubra levinodis* Nyl., which he describes as a typical member of the genus *Myrmica*.

Clausen's descriptions of *M. ruginodis* in copula state that the inner pair of male genital valves, the laminæ ædeagales, are inserted into the female's vagina from a dorsal, posterior position. This inverts the position of the ædeagus within the vagina so that the dorsal wall lies on the ventral surface of the vagina and the ventral serrate edges of the ædeagal valves contact the dorsal vaginal wall. The valves lie close together, and the sperm passageway is only along this now ventrally situated dorsal part of the inner valves. If the valves in *C. pennsylvanicus* take the same positions during copulation as those assumed by *M. ruginodis*, the sperm gutters which are described in this paper might be important in properly disposing the sperm within the female tract. At the present the purpose of these sperm gutters is not certain.

The ninth sterna or subgenital plates of the four species of the subgenus *Camponotus* compared in this paper are all similar in shape. Again for this segment there is a closer similarity between *pennsylvanicus* and *herculeanus* than between *pennsylvanicus* and the other species. An examination of the outlines

of the subgenital plates figured by Clausen for the different forms which he studied shows significant variations in the shape of this segment between subfamilies and genera. Smith (1943, pp. 276–278) has used the shape of the "hypopygium" for separating males of a few subfamilies. All this suggests that the shape of the ninth sternum has a value in separating subfamilies and genera. The minor variations of this segment might prove useful in separating subgenera and even species.

SUMMARY

This study describes and figures the external genitalic valves, the ninth and tenth abdominal terga, and the eighth and ninth sterna of the male Carpenter Ant, *C. pennsylvanicus* DeGeer.

The genitalic valves and the terminal segments of *pennsylvanicus* are similar in arrangement and shape to those of other described species of the genus.

Measurements are recorded for various parts of these structures, and *pennsylvanicus* is compared with species of *Camponotus* reported by Clausen (1938). The measurements place *pennsylvanicus* closer to *herculeanus* than to other species of the genus.

The genitalic valves of *pennsylvanicus,* in general, are longer and narrower than those of *herculeanus* with the exception of the length of the inner valve which is practically the same in both species.

A chitinous fold of the upper, median surface of each inner valve forms a furrow extending the length of the valve. This furrow is described for the first time. It is named the "sperm gutter" because of its position on the inner valve and because of its relation to the end of the ejaculatory duct.

Since no published account gives observations of species of *Camponotus* in copula, the positions of the genitalic valves in copulating pairs of the genus *Myrmica,* as described by Clausen, are discussed to outline the possible functions and the probable positions of the valves in *Camponotus* during copulation.

The shapes of the subgenital plates of ant subfamilies and genera show significant variations. This suggests that this segment might be of value in separating these taxonomic groups.

The minor variations of this segment might have importance for separating subgenera and even species.

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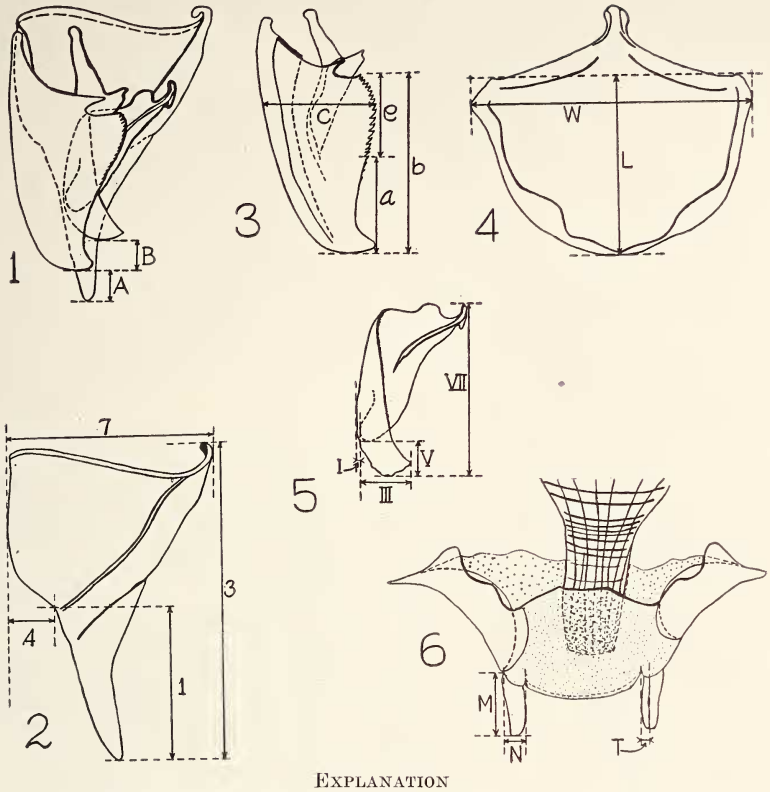
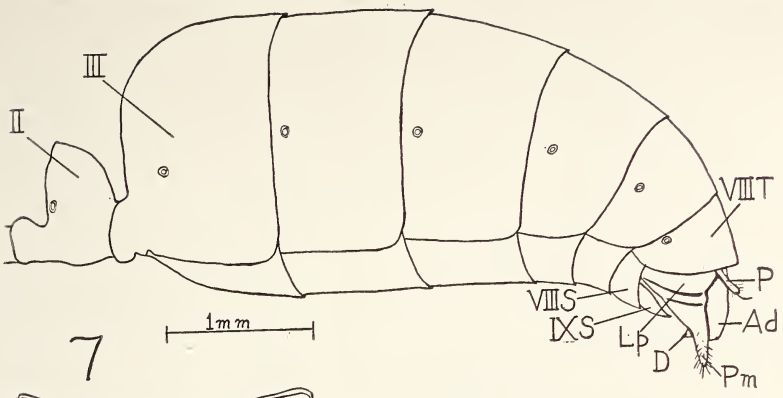


Explanation

The genitalic valves and terminal segments of *Camponotus pennsylvanicus* showing the scheme for measurements. Fig. 1, Median sagittal view of the genitalia which shows the three valves of one side in position: A, distance between caudal margins of the paramere and the lamina ædeagalis; B, distance between caudal margins of the lamina ædeagalis and the digitus volsellaris. Fig. 2, Lateral view of outer valve of genitalia: 1, length of paramere; 3, total length of outer valve; 4, distance between dorsal margins of the lamina parameralis and the paramere; 7, total width of outer valve. Fig. 3, Median view of inner valve, lamina ædeagalis: a, distance from caudal margin to the first distinct tooth; b, total length of ventral margin; c, width at right angles to b; e, length of serrate edge between first and last distinct tooth. Fig. 4, Ventral view of the subgenital plate, IXth sternum: L, length of subgenital plate excluding cranial projection; W, width of subgenital plate. Fig. 5, Median view of middle valve: I, distance between the dorsal margins of the cuspis volsellaris and the digitus volsellaris; III, distance between dorsal margin of cuspis volsellaris and the point of the digitus volsellaris; V, distance between caudal margins of cuspis volsellaris and digitus volsellaris; VII, total length of middle valve. Fig. 6, Dorsal view of the pygostyle-bearing Xth tergum: M, length of pygostyle; N, width of pygostyle; T, thickness of pygostyle on dorsal surface.

EXPLANATION OF PLATE XVI

FIG. 7, Lateral view of male gaster. Fig. 8, Dorsal view of genitalia. Fig. 9, Detailed lateral view of lamina ædeagalis, inner valve. Fig. 10, Detailed dorsal view of the IXth and Xth terga. Figures 8, 9, and 10 are drawn to the scale indicated at the lower left of the plate. II–III, 2nd and 3rd abdominal segments; VIIIT–IXT, 8th and 9th abdominal terga; VIIIS–IXS, 8th and 9th abdominal sterna; X, tenth or anal segment; A, anus; Aa, ædeagal apodeme; Ad, ædeagus; C, cuspis volsellaris; D, digitus volsellaris; Da, dorsal surface of ædeagus; L, lamina ædeagalis; La, lamina annularis or basal ring; Lp, lamina parameralis; M, anal muscle; P, pygostyle; Pm, paramere; R, rectum; S, sperm gutter.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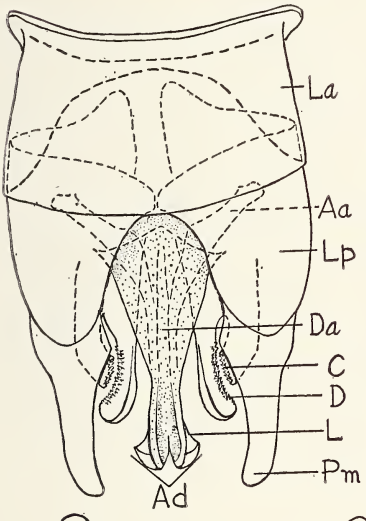
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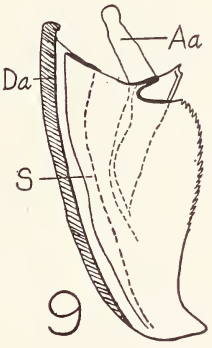
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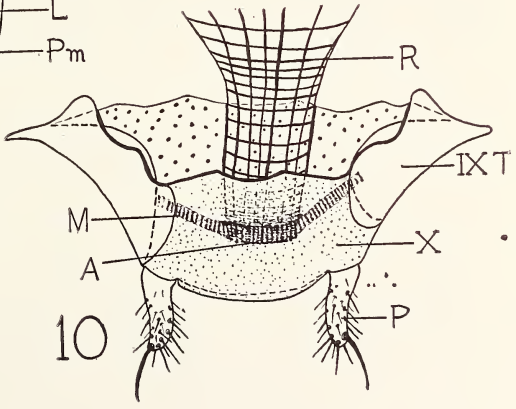
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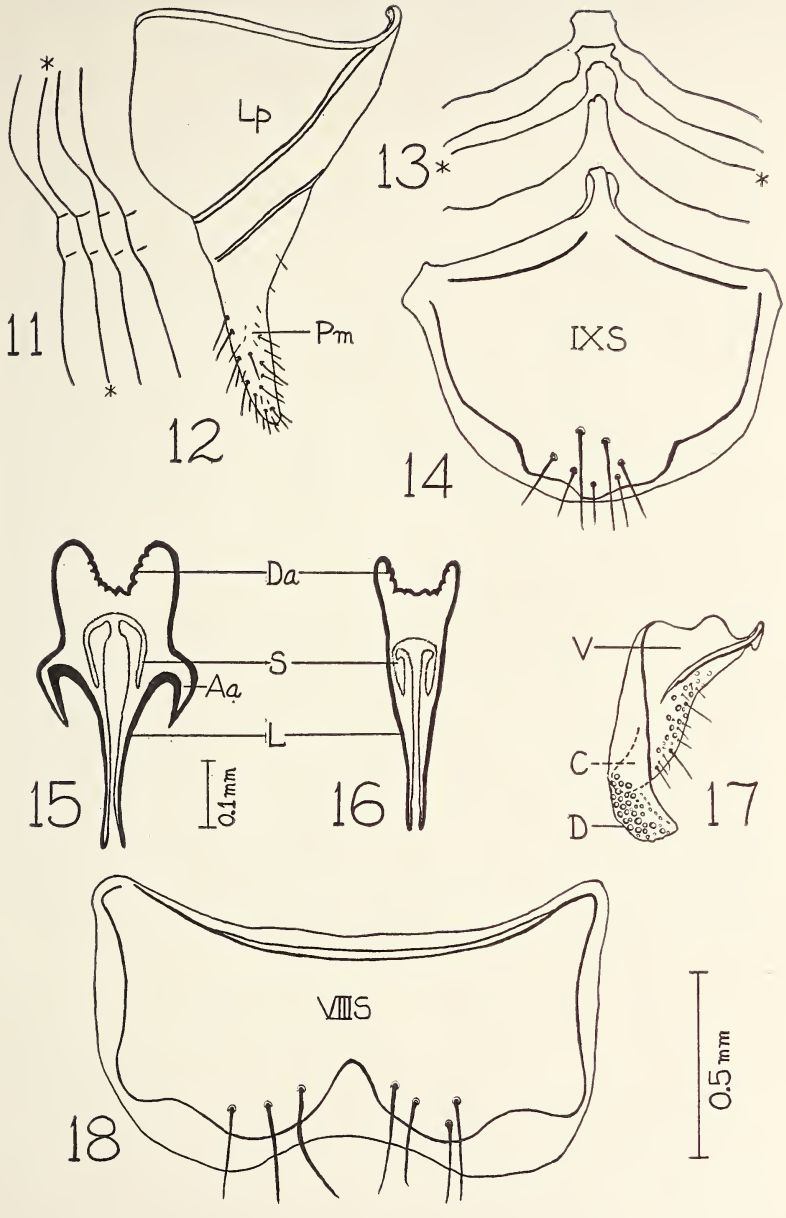
EXPLANATION OF PLATE XVII

FIG. 11, Outlines of various shapes of the dorsal margin of the outer valve —the one marked with * is the outline of fig. 12. Fig. 12, Detailed lateral view of the outer valve. Fig. 13, Outlines of various shapes of the cranial projection of the IXth sternum, the subgenital plate—the one marked with * is the outline of fig. 14. Fig. 14, Detailed ventral view of the IXth sternum. Fig. 15, Outline of a cross-sectional view of the ædeagus taken through the middle. Fig. 16, Outline of a cross-sectional view of the ædeagus taken through the beginning of the posterior third. (Figures 15 and 16 show the position of the sperm gutters on the median surfaces of the laminæ ædeagales.) Fig. 17, Detailed median view of the middle valve. Fig. 18, Detailed ventral view of the VIIIth sternum. Figures 12, 14, 17, and 18 are drawn to the scale indicated at the lower right of the plate. VIIIS–IXS, 8th and 9th abdominal sterna; Aa, ædeagal apodeme; C, cuspis volsellaris; D, digitus volsellaris; Da, dorsal surface of ædeagus; L, lamina ædeagalis; Lp, lamina parameralis; Pm, paramere; S, sperm gutter; V, lamina volsellaris.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